

A reduced estimate of the strength of the ocean's biological carbon pump

Stephanie A. Henson,¹ Richard Sanders,¹ Esben Madsen,² Paul J. Morris,³ Frédéric Le Moigne,¹ and Graham D. Quartly¹

Received 11 January 2011; accepted 19 January 2011; published 18 February 2011.

[1] A major term in the global carbon cycle is the ocean's biological carbon pump which is dominated by sinking of small organic particles from the surface ocean to its interior. Several different approaches to estimating the magnitude of the pump have been used, yielding a large range of estimates. Here, we use an alternative methodology, a thorium isotope tracer, that provides direct estimates of particulate organic carbon export. A large database of thorium-derived export measurements was compiled and extrapolated to the global scale by correlation with satellite sea surface temperature fields. Our estimates of export efficiency are significantly lower than those derived from the f -ratio, and we estimate global integrated carbon export as $\sim 5 \text{ GtC yr}^{-1}$, lower than most current estimates. The lack of consensus amongst different methodologies on the strength of the biological carbon pump emphasises that our knowledge of a major planetary carbon flux remains incomplete. **Citation:** Henson, S. A., R. Sanders, E. Madsen, P. J. Morris, F. Le Moigne, and G. D. Quartly (2011), A reduced estimate of the strength of the ocean's biological carbon pump, *Geophys. Res. Lett.*, 38, L04606, doi:10.1029/2011GL046735.

1. Introduction

[2] The oceans are a major repository for inorganic carbon [Siegenthaler and Sarmiento, 1993]. An important component of this sink is the biological carbon pump (BCP), driven by the sinking of small organic particles from the surface ocean to its interior [Falkowski et al., 1998; Sabine et al., 2004]. Of the organic material generated via primary production (PP) by phytoplankton in surface waters, most is recycled in the upper ocean. A small fraction is exported to depth and sequestered away from the atmosphere for hundreds to thousands of years. The magnitude of the BCP is predicted to decline in response to global climate change, resulting in reduced ocean carbon storage and hence increased atmospheric CO_2 levels [e.g., Matsumoto et al., 2010; Steinacher et al., 2010; Manizza et al., 2010]. Therefore, accurately quantifying the strength of the global BCP is essential to understanding the Earth's carbon cycle and, by extension, the impact of continued anthropogenic perturbation of atmospheric CO_2 levels.

[3] However, measuring the export flux of organic matter directly is challenging, so a common approach is to estimate

the fraction of the total PP that is eventually exported (i.e., the export efficiency). Total PP includes production fuelled by both 'new' and 'regenerated' nitrogen [Dugdale and Goering, 1967]. New production (NP) is assumed to be principally fuelled by nitrate supplied from depth by vertical mixing, whilst regenerated production (RP) is supported by the uptake of nitrogen derived from the recycling of organic matter in the euphotic zone. Over sufficiently large time and space scales, export production is equivalent to new production [Eppley and Peterson, 1979], so that the fraction of PP that is exported can be expressed as $\text{NP}/(\text{NP}+\text{RP})$, known as the f -ratio [Dugdale and Goering, 1967].

[4] The most widely used estimate of global carbon export is derived from a linear relationship between observed f -ratio and sea surface temperature (SST) [Laws et al., 2000]. Applying this to satellite-derived PP and SST fields yields an estimate of global carbon export of $\sim 12 \text{ GtC yr}^{-1}$. This is comparable to the 11 GtC yr^{-1} obtained from a food-web model [Laws et al., 2000], but substantially lower than global application of the earliest export algorithm (21 GtC yr^{-1}) [Eppley and Peterson, 1979].

[5] The empirical relationship derived in the Laws et al. [2000] study was based on f -ratio estimates from just 11 sites where comprehensive surveys of marine biogeochemistry had been conducted. At 7 of the 11 sites, f -ratio estimates were made using nitrogen isotope (^{15}N) experiments, which introduces an additional source of uncertainty [e.g., Fernandez and Raimbault, 2007]. This arises from the inherent assumption that all nitrate is supplied through wintertime mixing or upwelling of sub-surface waters, and that none is generated within the euphotic zone via the biologically mediated oxidation of ammonium (i.e., nitrification). At the time of Laws et al.'s [2000] study, nitrification was believed to occur almost entirely below the euphotic zone and thus contribute to the new nitrate pool. However, recent studies have demonstrated that nitrification rates are similar in surface and deep waters [Yool et al., 2007; Dore and Karl, 1996; Clark et al., 2008; Fernandez et al., 2009], suggesting that nitrification is an additional source of regenerated nitrate in the upper ocean. Indeed globally, nitrification in surface waters could supply up to half of the nitrate consumed by phytoplankton [Yool et al., 2007]. As a consequence, using the f -ratio to calculate export may result in an over-estimate of the magnitude of the BCP.

[6] An alternative approach to estimating particulate organic carbon (POC) export uses the particle tracer thorium-234 (^{234}Th). ^{234}Th is the radiogenic daughter product of the naturally occurring soluble isotope uranium-238 (^{238}U), which is proportionally conserved in seawater [Chen et al., 1986]. Unlike ^{238}U , ^{234}Th is insoluble in seawater and readily adheres to particulate matter. As particles sink, a

¹National Oceanography Centre, Southampton, UK.

²School of Applied Sciences, Cranfield University, Cranfield, UK.

³Woods Hole Oceanographic Institution, Woods Hole, Massachusetts, USA.

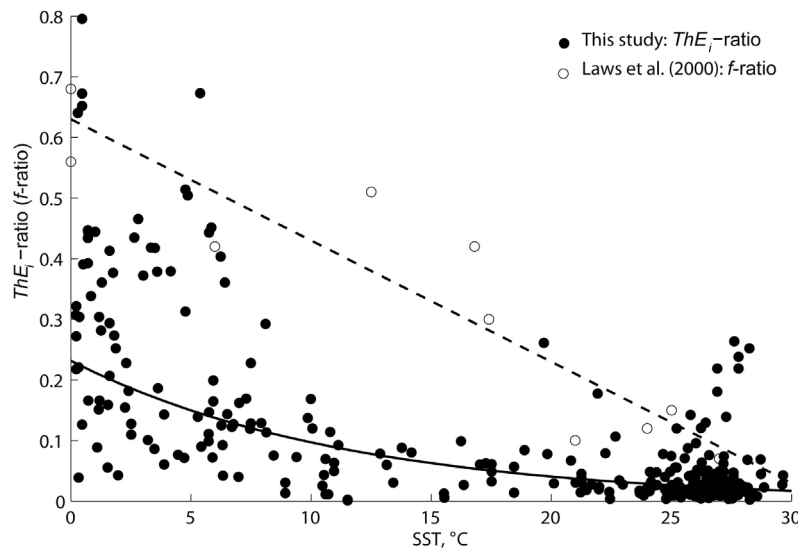


Figure 1. Relationship between sea surface temperature, ThE_i -ratio (solid circles) and f -ratio (open circles). ThE_i -ratio regression line is an exponential fit, $ThE_i\text{-ratio} = 0.23(\pm 0.04) \cdot \exp^{(-0.08(\pm 0.01) \cdot SST)}$, $r^2 = 0.50$, $p < 0.01$, $n = 306$; values in brackets are the 95% confidence limits on the regression coefficients. f -ratio regression line is a linear fit, $f\text{-ratio} = 0.63 - (0.02 \cdot SST)$ (data taken from Laws *et al.* [2000]).

radioactive disequilibrium between ^{238}U and ^{234}Th arises, and when combined with data on the particulate ratio of POC: ^{234}Th activity [Buesseler *et al.*, 2006], an estimate of POC export is obtained. An equivalent to the f -ratio for the efficiency of particle export is the ThE -ratio, defined as: ^{234}Th -derived export/PP [Buesseler, 1998].

[7] In order to estimate the total magnitude of the BCP, local measurements of export efficiency derived from the f - or ThE -ratio must be extrapolated to a global scale. Previous studies have demonstrated that SST is a good predictor of the f -ratio [Laws *et al.*, 2000; Wohlers *et al.*, 2009; Savoye *et al.*, 2004], as the balance between production and respiration is strongly affected by temperature. As one moves from cold, sub-polar regions into warm, sub-tropical waters, respiration declines more slowly than production [Duarte and Agusti, 1998], resulting in a decreasing f -ratio. Using SST as a predictor is also an appealing option, as satellite-derived SST data are widely available permitting the calculation of global export production estimates.

2. Methods

[8] For this study a database of ^{234}Th -derived export measurements was compiled from the literature (all details can be found in the auxiliary material).¹ All measurements are reported as the export at 100 m depth. Data from the Arctic and from shallow waters (<200 m depth) are excluded from the analysis. It should be noted that due to the predominance of open ocean thorium-export measurements in our dataset, our estimate of global carbon export does not explicitly parameterise the contribution from continental margins and shelves, potentially resulting in an underestimate of integrated export. However, the same is true of the f -ratio approach, and indeed almost all methodologies (an exception is that of Schlitzer [2000]), so our results remain directly comparable with previous estimates.

[9] ThE -ratio estimates are typically made using *in situ* PP measured during 12 or 24 hour incubations. However, the residence time of ^{234}Th is considered to be ~2–20 days [Coale and Bruland, 1985] (shorter than its mean life of 24 days, due to scavenging), and therefore the export estimated using this method represents an integrated value over days to a couple of weeks. This introduces a mismatch in time scales with the instantaneous PP measured *in situ*. Here we account for the integration time scale of the ^{234}Th -derived export by using the integrated satellite-derived PP over the 16 days prior to the *in situ* measurement. We term this the integrated thorium export ratio, ThE_i -ratio, to distinguish it from the original definition of the ThE -ratio based on instantaneous PP [Buesseler, 1998].

[10] Climatological 8-day composites of Level-3 SeaWiFS chlorophyll-*a* concentration, photosynthetically available radiation and AVHRR SST data were downloaded from <http://oceancolor.gsfc.nasa.gov> and <http://pathfinder.node.noaa.gov/>, respectively. All data were spatially averaged to a 1° grid. PP was derived from satellite data using the 3 principal algorithms (a detailed intercomparison of several PP algorithms is given by Carr *et al.* [2006]): the Vertically Generalized Production Model [Behrenfeld and Falkowski, 1997], Marra *et al.* [2003] and Carr's [2001] algorithms and multiplied by the ThE_i -ratio to estimate particle export. Although PP is used to estimate both ThE_i -ratio and export, both the time (16-day vs. annual integral PP) and space (point observations of thorium-derived export vs. globally-resolved PP) scales are different. The *in situ* thorium export measurements listed in Table S1 (see auxiliary material) were compared with the corresponding satellite-derived export, calculated using each of the three PP algorithms. Carr's [2001] algorithm was chosen for its ability to replicate the *in situ* export measurements with the lowest root mean square error and highest r^2 . The error on the estimate of globally integrated carbon export is reported as the median relative error of measured versus predicted POC flux (=55%). This incorporates all the errors associated with the satellite-derived

¹Auxiliary materials are available in the HMTL. doi:10.1029/2011GL046735.

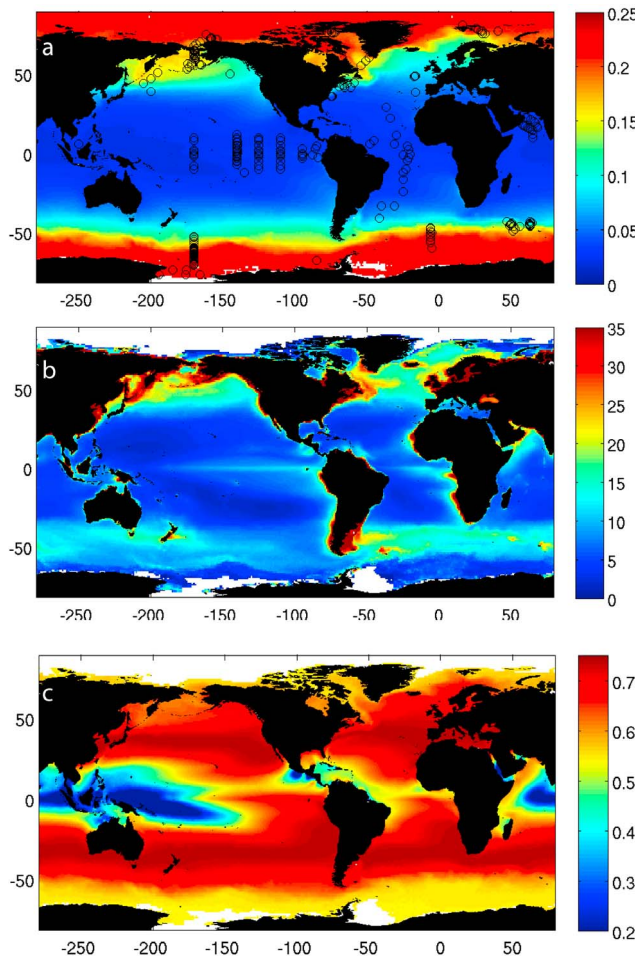


Figure 2. (a) ThE_i -ratio estimated from relationship shown in Figure 1. Circles mark location of *in situ* ^{234}Th measurements. (b) POC export ($gC\ m^{-2}\ yr^{-1}$) derived from ThE_i -ratio and satellite primary production (global integrated total 4 $GtC\ yr^{-1}$). (c) Fractional difference between the f -ratio and ThE_i -ratio, calculated as $(f\text{-ratio} - ThE_i\text{-ratio})/(f\text{-ratio})$.

estimates of PP and SST, plus the error arising from an imperfect ThE_i -ratio to SST relationship. The error estimate does not however include systematic uncertainties associated with the thorium technique itself, such as the POC:Th ratio and steady state assumptions, and so is likely an underestimate.

[11] The f -ratio based export is estimated using the relationship between SST and the f -ratio derived from data in Table 3 of Laws *et al.* [2000]:

$$f - ratio = 0.62 - (0.02 * SST) \quad (1)$$

Both the ThE_i -ratio versus SST relationship derived here, and the f -ratio versus SST relationship above, were applied to the same satellite-derived PP fields to calculate export, so that the relative difference between the two estimates is not dependent on the choice of satellite PP algorithm.

3. Results

[12] The ThE_i -ratio calculated using the 16-day integrated PP is plotted against SST in Figure 1. Sub-tropical waters

have ThE_i -ratios in the range of ~ 0.01 to 0.2 , and temperate and sub-polar northern hemisphere waters have ThE_i -ratios between ~ 0.1 and 0.3 . In the Southern Ocean ($SST < 7^\circ C$), the ThE_i -ratio varies widely from ~ 0.1 to 0.7 . Also plotted in Figure 1 is the f -ratio and SST data of Laws *et al.* [2000, Table 3]. Despite the considerable scatter in the ThE_i -SST plot, the two relationships are clearly different, with the ThE_i -ratio consistently lower than the f -ratio, particularly at mid-latitudes ($SST \sim 7\text{--}20^\circ C$).

[13] Fitting an exponential function to the ThE_i -SST data produces the relationship ($r^2 = 0.5$, $p < 0.01$):

$$ThE_i - ratio = 0.23 \exp^{(-0.08 * SST)} \quad (2)$$

From a metabolic standpoint, an exponential relationship is more apposite than a linear fit, as the balance between respiration and production, which effectively drives the fraction of PP that is exported, is an exponential function of temperature [Lopez-Urrutia *et al.*, 2006].

[14] Much of the scattered Southern Ocean data comes from a transect from the Polar Front to the retreating ice edge in the Ross Sea [Buesseler *et al.*, 2003]. The large range of ThE_i -ratio values found there was attributed by the authors to the very different phytoplankton community structures encountered during the transect, indicating an important secondary control over ThE_i -ratios. An additional contributor to the scatter may be the spatial variability in thorium export, that varies on scales of 'tens to hundreds of kilometres' [Buesseler *et al.*, 2009], i.e., potentially smaller than the 1° satellite data used here. Seasonal variability may also play a role, through phytoplankton succession and changes in ecosystem structure, nutrient availability and PP itself [Boyd and Trull, 2007]. Despite the scatter introduced by these factors, and the simplicity of the relationship, SST alone is still able to explain 50% of the variance in the ThE_i -ratio.

[15] A global map of the annual mean ThE_i -ratio (Figure 2a) shows the expected pattern of low ThE_i -ratios at low latitudes (between $40^\circ N$ and $40^\circ S$), moderate values in northern hemisphere high latitudes and high ThE_i -ratios in the Southern Ocean. The export of POC calculated from multiplying the ThE_i -ratio by PP is shown in Figure 2b. POC export in the Northern Hemisphere high latitudes is $\sim 25\text{--}30\ gC\ m^{-2}\ yr^{-1}$, contrasting with similar latitudes in the Southern Ocean, where export is estimated at $\sim 5\text{--}10\ gC\ m^{-2}\ yr^{-1}$. The low latitudes have an export of $\sim 1\text{--}5\ gC\ m^{-2}\ yr^{-1}$, with higher values ($\sim 10\text{--}15\ gC\ m^{-2}\ yr^{-1}$) in upwelling regions. The annually integrated global POC export derived from the ThE_i -ratio is $4 (\pm 2.2)\ GtC\ yr^{-1}$. This is two-thirds less than the export estimated using the f -ratio to SST relationship of Laws *et al.* [2000] ($\sim 12\ GtC\ yr^{-1}$). Why is there such a large difference between export estimated from thorium measurements and that estimated from the f -ratio?

4. Discussion

[16] Part of the discrepancy between ThE_i - and f -ratio based estimates of export arises because the thorium approach only accounts for the export of particulate organic carbon. Contributions to export flux also come from the production, seasonal accumulation, subduction and respiration of dissolved organic carbon (DOC). As a global average, the contribution of DOC to global export in the open ocean is $\sim 20\%$ [Hansell and Carlson, 1998]. Adding

in this contribution brings our estimate of globally integrated export to 5 GtC yr^{-1} , still $\sim 60\%$ lower than the f -ratio based estimate.

[17] Part of the difference between the ThE_f - and f -ratio estimates is likely due to nitrification in the upper ocean, which results in some production previously considered to be new, now being considered recycled [Yool *et al.*, 2007; Dore and Karl, 1996; Diaz and Raimbault, 2000]. The fractional difference between the ThE_f -ratio and the f -ratio is highest in the oligotrophic gyres and lower in the Southern Ocean and equatorial regions (Figure 2c). The relatively small difference between f - and ThE_f -ratio at high latitudes and in equatorial regions suggests that the majority of production here is fuelled by new nutrients supplied by vertical transport, and that the contribution of nitrification is minor. At low latitudes, however, the large difference between f - and ThE_f -ratio estimates suggests that nitrate regeneration by nitrification may comprise a substantial fraction of the euphotic zone nitrate pool in these regions. These spatial differences are consistent with *in situ* measurements of nitrification rates, which were estimated as supplying 2–16% of the total nitrate pool in the Peruvian upwelling [Fernandez *et al.*, 2009], 20–40% of it in the temperate North Atlantic [Fernandez and Raimbault, 2007], and a “substantial majority” of it in the oligotrophic Atlantic [Clark *et al.*, 2008].

[18] Whilst upper ocean nitrification potentially results in the f -ratio approach over-estimating export efficiency, additional uncertainty arises from nitrogen fixation, the process by which atmospheric N_2 is converted into ammonium. The magnitude of this source of new nitrate was unknown at the time the f -ratio was originally defined, but current estimates suggest that global marine N_2 fixation is $\sim 120 \text{ TgN yr}^{-1}$ [Codispoti *et al.*, 2001; Gruber, 2004], equivalent to $\sim 0.8 \text{ GtC yr}^{-1}$, assuming Redfield stoichiometry. As a consequence of N_2 fixation, using the f -ratio to calculate carbon export may result in an underestimate of $\sim 7\%$. The overestimate of carbon export due to nitrification (by up to 50% [Yool *et al.*, 2007]) is, on a global scale, larger than the underestimate arising from N_2 fixation. This implies that the overall effect of using the f -ratio to calculate global export results in an overestimate of the magnitude of the BCP.

[19] Other approaches to estimating global carbon export suggest values ranging from $\sim 5.7 \text{ GtC yr}^{-1}$ [Lutz *et al.*, 2007] to $\sim 20 \text{ GtC yr}^{-1}$ [Eppley and Peterson, 1979], with several estimates clustering around $10\text{--}12 \text{ GtC yr}^{-1}$ [Dunne *et al.*, 2007; Schlitzer, 2004; Laws *et al.*, 2000]. It has been suggested that even the higher values are too low to balance the respiration by heterotrophic activity occurring in meso- and bathypelagic waters [Burd *et al.*, 2010; del Giorgio and Duarte, 2002]. Estimates of export made at HOTS and BATs on the basis of oxygen or carbon isotope mass balance are ~ 5 times greater than those made here [Emerson *et al.*, 2001]. Our global export estimate overlaps with that of Lutz *et al.* [2007], but is significantly lower than other previous estimates. Why do different methodologies arrive at such a wide range of estimates?

[20] The various approaches to estimating global carbon export each have their own sources of uncertainty, in addition to an issue common to all of the methods, that of sparse *in situ* data that, generally speaking, are unable to sample temporal or spatial variability. Episodic export events, seasonal and interannual variability, and spatial patchiness in

particle export are not usually resolved. Scaling up these point measurements to create a global budget assumes that the data are truly representative of normal conditions, i.e., a degree of spatial and temporal homogeneity has to be assumed.

[21] In addition, there are sources of uncertainty specific to each approach for estimating export. The thorium method relies on determination of the $POC:^{234}Th$ ratio, which can vary by sampling method, regionally and with depth [Buesseler *et al.*, 2006]. Applying the f -ratio approach requires careful accounting of new and regenerated sources of nitrate, including nitrification, N_2 fixation and atmospheric deposition. Estimating global-scale export from meso- and bathypelagic respiration entails large uncertainties in the measurements, particularly bacterial growth efficiency and cell carbon content [Burd *et al.*, 2010]. Additional poorly characterised terms in the estimation of carbon export arise from horizontal advection of material [Benitez-Nelson *et al.*, 2000] and active transport of carbon by zooplankton [Steinberg *et al.*, 2000].

[22] The discrepancies between our thorium-based approach, the f -ratio method and mesopelagic metabolic activity suggest that we may be overlooking significant sources or sinks of carbon, or that there are problems with one or more of the measurement methodologies. What is clear is that our knowledge of a major planetary carbon flux is incomplete, and that continued research will be essential to our understanding of the role of upper ocean export in the global carbon cycle and regulation of atmospheric CO_2 .

[23] **Acknowledgments.** Thanks to Ken Buesseler and Kanchan Maiti for useful discussions on the thorium technique and supplying additional thorium export data. SeaWiFS data were provided by GSFC/NASA in accordance with the SeaWiFS Research Data Use Terms and Conditions Agreement. The AVHRR Oceans Pathfinder SST data were obtained from the Physical Oceanography Distributed Active Archive Center (PO.DAAC) at the NASA Jet Propulsion Laboratory.

[24] P. G. Strutton thanks two anonymous reviewers.

References

- Behrenfeld, M. J., and P. G. Falkowski (1997), Photosynthetic rates derived from satellite-based chlorophyll concentration, *Limnol. Oceanogr.*, **42**(1), 1–20, doi:10.4319/lo.1997.42.1.0001.
- Benitez-Nelson, C., K. O. Buesseler, and G. Crossin (2000), Upper ocean carbon export, horizontal transport and vertical eddy diffusivity in the southwestern Gulf of Maine, *Cont. Shelf Res.*, **20**, 707–736, doi:10.1016/S0278-4343(99)00093-X.
- Boyd, P. W., and T. W. Trull (2007), Understanding the export of biogenic particles in oceanic waters: Is there consensus?, *Prog. Oceanogr.*, **72**, 276–312, doi:10.1016/j.pocean.2006.10.007.
- Buesseler, K. O. (1998), The decoupling of production and particulate export in the surface ocean, *Global Biogeochem. Cycles*, **12**(2), 297–310, doi:10.1029/97GB03366.
- Buesseler, K. O., R. T. Barber, M. L. Dickson, M. R. Hiscock, J. K. Moore, and R. Sambrotto (2003), The effect of marginal ice-edge dynamics on production and export in the Southern Ocean along 170 degrees W, *Deep Sea Res., Part II*, **50**(3–4), 579–603, doi:10.1016/S0967-0645(02)00585-4.
- Buesseler, K. O., et al. (2006), An assessment of particulate organic carbon to thorium-234 ratios in the ocean and their impact on the application of $Th-234$ as a POC flux proxy, *Mar. Chem.*, **100**(3–4), 213–233, doi:10.1016/j.marchem.2005.10.013.
- Buesseler, K. O., S. M. Pike, K. Maiti, C. Lamborg, D. A. Siegel, and T. W. Trull (2009), Thorium-234 as a tracer of spatial, temporal and vertical variability in particle flux in the North Pacific, *Deep Sea Res., Part I*, **56**(7), 1143–1167, doi:10.1016/j.dsr.2009.04.001.
- Burd, A. B., et al. (2010), Assessing the apparent imbalance between geochemical and biochemical indicators of meso- and bathypelagic biological activity: What the @\\$#! is wrong with present calculations of carbon budgets?, *Deep Sea Res., Part II*, **57**(16), 1557–1571, doi:10.1016/j.dsr.2010.02.022.

- Carr, M.-E. (2001), Estimation of potential productivity in Eastern Boundary Currents using remote sensing, *Deep Sea Res., Part II*, 49(1–3), 59–80, doi:10.1016/S0967-0645(01)00094-7.
- Carr, M.-E., et al. (2006), A comparison of global estimates of marine primary production from ocean color, *Deep Sea Res., Part II*, 53(5–7), 741–770, doi:10.1016/j.dsr2.2006.01.028.
- Chen, J. H., R. L. Edwards, and G. J. Wasserburg (1986), ^{238}U , ^{234}U and ^{232}Th in seawater, *Earth Planet. Sci. Lett.*, 80(3–4), 241–251, doi:10.1016/0012-821X(86)90108-1.
- Clark, D. R., A. P. Rees, and I. Joint (2008), Ammonium regeneration and nitrification rates in the oligotrophic Atlantic Ocean: Implications for new production estimates, *Limnol. Oceanogr.*, 53(1), 52–62, doi:10.4319/lo.2008.53.1.0052.
- Coale, K. H., and K. W. Bruland (1985), ^{234}Th : ^{238}U disequilibria within the California Current, *Limnol. Oceanogr.*, 30(1), 22–33, doi:10.4319/lo.1985.30.1.0022.
- Codispoti, L. A., J. A. Brandes, J. P. Christensen, A. H. Devol, S. W. A. Naqvi, H. W. Paerl, and T. Yoshinari (2001), The oceanic fixed nitrogen and nitrous oxide budgets: Moving targets as we enter the anthropocene?, *Sci. Mar.*, 65, 85–105.
- del Giorgio, P. A., and C. M. Duarte (2002), Respiration in the open ocean, *Nature*, 420(6914), 379–384, doi:10.1038/nature01165.
- Díaz, F., and P. Raimbault (2000), Nitrogen regeneration and dissolved organic nitrogen release during spring in a NW Mediterranean coast zone (Gulf of Lions): Implications for the estimation of new production, *Mar. Ecol. Prog. Ser.*, 197, 51–65, doi:10.3354/meps197051.
- Dore, J. E., and D. M. Karl (1996), Nitrification in the euphotic zone as a source for nitrite, nitrate and nitrous oxide at Station ALOHA, *Limnol. Oceanogr.*, 41(8), 1619–1628, doi:10.4319/lo.1996.41.8.1619.
- Duarte, C. M., and S. Agusti (1998), The CO_2 balance of unproductive aquatic ecosystems, *Science*, 281(5374), 234–236, doi:10.1126/science.281.5374.234.
- Dugdale, R. C., and J. J. Goering (1967), Uptake of new and regenerated forms of nitrogen in primary productivity, *Limnol. Oceanogr.*, 12(2), 196–206, doi:10.4319/lo.1967.12.2.0196.
- Dunne, J. P., J. L. Sarmiento, and A. Gnanadesikan (2007), A synthesis of global particle export from the surface ocean and cycling through the ocean interior and on the seafloor, *Global Biogeochem. Cycles*, 21, GB4006, doi:10.1029/2006GB002907.
- Emerson, S., S. Mecking, and J. Abell (2001), The biological pump in the subtropical North Pacific Ocean: Nutrient sources, Redfield ratios and recent changes, *Global Biogeochem. Cycles*, 15, 535–554, doi:10.1029/2000GB001320.
- Eppley, R. W., and B. J. Peterson (1979), Particulate organic matter flux and planktonic new production in the deep ocean, *Nature*, 282(5740), 677–680, doi:10.1038/282677a0.
- Falkowski, P. G., R. T. Barber, and V. Smetacek (1998), Biogeochemical controls and feedbacks on ocean primary production, *Science*, 281(5374), 200–206, doi:10.1126/science.281.5374.200.
- Fernandez, C., and P. Raimbault (2007), Nitrogen regeneration in the NE Atlantic Ocean and its impact on seasonal new, regenerated and export production, *Mar. Ecol. Prog. Ser.*, 337, 79–92, doi:10.3354/meps337079.
- Fernandez, C., L. Farias, and M. E. Alcaman (2009), Primary production and nitrogen regeneration processes in surface waters of the Peruvian upwelling system, *Prog. Oceanogr.*, 83(1–4), 159–168, doi:10.1016/j.pcean.2009.07.010.
- Gruber, N. (2004), The dynamics of the marine nitrogen cycle and its influence on atmospheric CO_2 , in *Carbon-Climate Interactions*, edited by M. Follows and T. Oguz, pp. 97–148, Kluwer Acad., Dordrecht, Netherlands.
- Hansell, D. A., and C. A. Carlson (1998), Net community production of dissolved organic carbon, *Global Biogeochem. Cycles*, 12(3), 443–453, doi:10.1029/98GB01928.
- Laws, E. A., P. G. Falkowski, W. O. Smith, H. Ducklow, and J. J. McCarthy (2000), Temperature effects on export production in the open ocean, *Global Biogeochem. Cycles*, 14(4), 1231–1246, doi:10.1029/1999GB001229.
- Lopez-Urrutia, A., E. San Martin, R. P. Harris, and X. Irigoien (2006), Scaling the metabolic balance of the oceans, *Proc. Natl. Acad. Sci. U. S. A.*, 103(23), 8739–8744, doi:10.1073/pnas.0601137103.
- Lutz, M. J., K. Caldeira, R. B. Dunbar, and M. J. Behrenfeld (2007), Seasonal rhythms of net primary production and particulate organic carbon flux to depth describe the efficiency of the biological pump in the global ocean, *J. Geophys. Res.*, 112, C10011, doi:10.1029/2006JC003706.
- Manizza, M., E. T. Buitenhuis, and C. Le Quere (2010), Sensitivity of global ocean biogeochemical dynamics to ecosystem structure in a future climate, *Geophys. Res. Lett.*, 37, L13607, doi:10.1029/2010GL043360.
- Marra, J., C. Ho, and C. C. Trees (2003), An alternative algorithm for the calculation of primary production from remote sensing data, *LDEO Tech. Rep. 2003-1*, Lamont-Doherty Earth Obs., Palisades, N. Y.
- Matsumoto, K., K. S. Tokos, M. O. Chikamoto, and A. Ridgwell (2010), Characterizing post-industrial changes in the ocean carbon cycle in an Earth system model, *Tellus, Ser. B*, 62(4), 296–313, doi:10.1111/j.1600-0889.2010.00461.x.
- Sabine, C. L., et al. (2004), The oceanic sink for anthropogenic CO_2 , *Science*, 305(5682), 367–371, doi:10.1126/science.1097403.
- Savoye, N., F. Dehairs, M. Elskens, D. Cardinal, E. E. Kopczynska, T. W. Trull, S. Wright, W. Baeyens, and F. B. Griffiths (2004), Regional variation of spring N-uptake and new production in the Southern Ocean, *Geophys. Res. Lett.*, 31(3), L03301, doi:10.1029/2003GL018946.
- Schlitzer, R. (2000), Applying the adjoint method for global biogeochemical modeling, in *Inverse Methods in Global Biogeochemical Cycles*, *Geophys. Monogr. Ser.*, vol. 114, edited by P. Kasibhatla et al., pp. 107–124, AGU, Washington, D. C.
- Schlitzer, R. (2004), Export production in the equatorial and North Pacific derived from dissolved oxygen, nutrient and carbon data, *J. Oceanogr.*, 60(1), 53–62, doi:10.1023/B:JOCE.0000038318.38916.e6.
- Siegenthaler, U., and J. L. Sarmiento (1993), Atmospheric carbon dioxide and the ocean, *Nature*, 365(6442), 119–125, doi:10.1038/365119a0.
- Steinacher, M., et al. (2010), Projected 21st century decrease in marine productivity: A multi-model analysis, *Biogeosciences*, 7(3), 979–1005, doi:10.5194/bg-7-979-2010.
- Steinberg, D. K., C. A. Carlson, N. R. Bates, S. A. Goldthwait, L. P. Madin, and A. F. Michaels (2000), Zooplankton vertical migration and the active transport of dissolved organic and inorganic carbon in the Sargasso Sea, *Deep Sea Res., Part I*, 47(1), 137–158, doi:10.1016/S0967-0637(99)00052-7.
- Wohlers, J., A. Engel, E. Zoellner, P. Breithaupt, K. Juergens, H.-G. Hoppe, U. Sommer, and U. Riebesell (2009), Changes in biogenic carbon flow in response to sea surface warming, *Proc. Natl. Acad. Sci. U. S. A.*, 106(17), 7067–7072, doi:10.1073/pnas.0812743106.
- Yool, A., A. P. Martin, C. Fernandez, and D. R. Clark (2007), The significance of nitrification for oceanic new production, *Nature*, 447(7147), 999–1002, doi:10.1038/nature05885.

S. A. Henson, F. Le Moigne, G. D. Quartly, and R. Sanders, National Oceanography Centre, European Way, Southampton SO14 3ZH, UK. (s.henson@noc.soton.ac.uk)

E. Madsen, School of Applied Sciences, Cranfield University, College Road, Cranfield MK43 0AL, UK.

P. J. Morris, Woods Hole Oceanographic Institution, 266 Woods Hole Rd., Woods Hole, MA 02543, USA.